8 Species diversity and the structure of microbial communities in terrestrial habitats

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Introduction

The last decade has seen an increasing involvement of microbiologists in integrated ecological research programmes such as those promoted by the IBP. As a result of this much firmer statements can be made than previously concerning the quantitative role of micro-organisms within natural ecosystems. The role of microbes in the energy transformations and nutrient cycling of terrestrial and aquatic systems are described elsewhere in this volume (Hissett, Ausmus, Dowding, Saunders, Fenchell). In addition it has been possible to establish more clearly the trophic relationships between micro-organisms and other components of the decomposer biota (Wiegert *et al.* 1970; Heal & MacLean in press).

In the majority of these studies, however, it has only proved possible to deal with the microflora as a single entity, or at best to subdivide it into its major components (fungi, bacteria, actinomycetes). Yet the microflora associated with dead plant or animal materials may be extremely diverse. For instance Novack & Whittingham (1968) described 161 species of fungi on the mixed deciduous leaf litter of a single woodland, Hayes (1965) found 120 species on needles of *Pinus sylvestris* and Frankland (1966) found 113 on petioles of *Pteridium aquilinum*. Comparable numbers of species have been recorded for other microbial groups and on other types of organic material.

The interactions between these microbial species and their patterns of distribution may be important factors in determining rates and patterns of decomposition. It is the purpose of this paper to review some of the current concepts of the functional roles of different components of the microbial communities associated with the decomposition of plant matter in terrestrial habitats and to propose some aspects of the structure of such com-

munities. In doing this I shall draw mainly on information derived from patterns of distribution of species in space and time. Questions of species abundance, trophic relationships between species or their symbiotic or competitive interaction will only be touched on. Thus 'diversity' in the context of this paper relates usually to species number rather than carrying any implications of equitability or of abundance. In carrying out such an analysis a number of fundamental problems of microbial ecology must be considered.

THE DETERMINATION OF SPECIES COMPOSITION

Any attempt to discuss the species composition of a microbial community is fraught with dangers of many kinds. The methods of detection and determination of microbial species are all highly selective. The species list derived for any habitat will have two characteristics which are a consequence of these problems of method. It will be incomplete, and it will be biased in respect of some physiological feature selected for by the method. In addition most isolation techniques do not distinguish between the actively growing decomposer or the resting-spore of an 'invader'. These difficulties have been discussed many times and nowhere more informatively than by Warcup (1965). Qualification must thus be made to any generalization made in terms of a species list of micro-organisms.

In the bacteria and the actinomycetes the concept of what is a species is itself by no means a matter of general acceptance (e.g. see Gray 1969, Williams *et al.* 1969, Szabo 1974). The lack of readily recognizable morphological diversity has led to the utilization of a series of biochemical and physiological features to distinguish taxa. This leads to a merging of taxonomic status and ecological function which can be confusing in some circumstances, enlightening in others. The fungi have a clearer taxonomic structure—(but see Hudson 1970)—and readily gain major prominence in this discussion. Most of the examples are drawn from woodland habitats of temperate regions which lends potential consistency to the argument but introduces inevitable bias.

Despite these reservations and qualifications it is the thesis of this review that the patterns of distribution of microbial species in space and time are informative and provide a framework within which the functioning of individual species populations of decomposers can be instructively investigated.

THE QUESTION OF SCALE IN TIME AND SPACE

Analysis of the structure within communities depends on the recognition of pattern in the distribution of the component species in space and time.

It is a feature of all communities, but particularly so for microbial communities, that the scale at which its features are observed determines the patterns that are deduced. Burges (1960) emphasized how easy it was to be misled if techniques of investigation were used in a scale of dimension for which they were not devised. The integrated studies of the IBP have also exposed the dangers of losing sight of scale differences. The multiplication of data derived by microbiologists from a few grammes of soil, to derive data on a per hectare basis ignores all potential scales of pattern between these two and runs the risk of producing absurd results. Patterns of microbial distribution and activity may also be expressed over widely differing scales in time, ranging from the evolutionary development of the microflora characteristic of a particular soil, to the responses of populations to environmental fluctuations with scales in hours or minutes.

It is clearly of particular importance to the understanding of the role of micro-organisms at the ecosystem level that the scale in space and time of any described microbial process be fully appreciated. A structure for microbial communities can be obtained by describing the spatial patterns of species distribution and the ways in which they change with time.

Patterns of distribution in space

The spatial structure of decomposer communities is primarily determined by the nature of the food resources on which they depend. The heterogeneous nature of the primary food resource, the dead organic material of plant origin, accounts for a large proportion of the observed diversity in microbial species. This resource may be categorized in terms of the plant organ from which it is derived (leaves, stems, roots, fruits etc.) each with differing physical and chemical structures and distributions in time and space. These structures are sometimes described as 'substrates'; this usage however conflicts with the biochemical definition of a chemical entity that interacts in a specific manner with an enzyme. I would, therefore, propose that the term '*primary resource*' be used as the generic term at the morphological level. In the same way *secondary resources* may be used for materials originating from secondary production which become food resources for decomposer organisms. These include all dead animal and microbial tissues. Decaying vegetation quickly becomes a mixture of both primary and secondary resources; much of the faecal material of soil animals is an intimate mixture of both. Thus the distinction may quickly lose its practical usefulness in the face of an inability to distinguish the interwoven patterns of distribution. However, I would suggest that the distinction is useful conceptually

and that many of the arguments applied below to the primary resources and their selective influence on the microflora may also be widened to include the secondary resources.

DISTRIBUTION OF MICROBIAL SPECIES IN RELATION TO PRIMARY RESOURCES

A comprehensive analysis of the microflora of decaying plant debris will yield many hundreds of species. An initial partitioning of this community can be readily made on the basis of specificity for the different types of primary resource. Thus there is a recognizably different fungal flora of leaves and branch-wood about which some taxonomic generalizations can be made; for instance the Aphyllophorales and Xylariaceous Ascomycetes commonly found on decaying wood are absent from leaf litter. The nature of this specialization is unclear; one possible relationship may be the size of the resource in relation to the energy demand for fruit-body production in these particular groups. This is emphasized further by the observation that the microflora of twigs may be very different from that of large branch-wood. However, whilst size may be a selection factor, other features may be of greater importance.

The selective effect of primary resource types on microfungi is illustrated by the work of Caldwell (1963); when segments of root and twig of beech of approximately similar dimensions were buried in the same soil they were colonized by different components of the mycoflora. Of the fourteen genera and seven species of microfungi identified in one experiment, nine genera and six species were resource specific. However, some overlap between different types of resources is common and many microfungi may be found on a variety of different plant tissues. This distinction between *resource-specific* (RS) and *nonspecific* (RN) species is also seen when any one type of resource is examined for microbial distribution patterns in relation to plant species of origin. Hering (1965) isolated or identified eighty-two species of fungi associated with mixed deciduous leaf litter. Details were given for the distribution of fifty of the species and these data are summarized in Table 8.1. The fungi were partitioned between the species of leaves in such a way that about half the recorded species were only found on one of the four leaf types. Conversely over 40% occurred on at least three of the four species of leaf. On this basis the fungal flora can be subdivided into RS and RN groups. This behaviour is not confined to the fungi; for instance Hissett & Gray (1974) found that of twelve species—groups of bacteria isolated from leaf litter in a mixed deciduous woodland, five were found on ash alone, two on oak alone and five were common to both.

Table 8.1. The distribution of species of fungi between four species of leaf (=four different primary resources) in the litter layer of an oak wood. Data re-calculated from Hering (1965).

	Numbers of Species			
1. Total Species	50			
	Ash	*Birch*	*Hazel*	*Oak*
2. Distribution between resources	28	28	23	31
3. Resource specific (RS)	8	6	2	10
4. Total RS	26			
5. Resource non-specific (RN)				
(a) All resources	15			
(b) Three resources	6*			

*A further three species were found on two of the leaf types.

The basis of such resource-specificity is not well understood but is generally attributed to the presence of specific chemicals (= modifiers, see p. 193). For instance the distribution of wood decay fungi between different types of timber has been attributed to the presence of a variety of organic chemicals including terpenes and polyphenols (Hintikka 1970; Scheffer & Cowling 1966). Comparable evidence is not available for decomposer microbes on other materials. However, the selective effect of roots on the soil microflora is well documented and is attributed to the presence of specific substances in root exudates (Chan *et al.* 1963). As the organisms from the rhizosphere are among the primary colonisers and decomposers of roots (Dix 1964; Waid 1974) the selective activity of the living root may well determine the nature of the subsequent decomposer microflora. This effect may also be seen in other resources where the initial decomposer microflora often spans both parasitic and saprophytic phases.

The composition of the RN microflora deserves further mention. Many of these organisms have an extremely wide resource distribution. For instance of the fifteen species of fungi* found on all four species of leaf litter by Hering (see Table 8.1), seven were found on beech branch wood by myself,[1] eleven on *Pteridium* petioles by Frankland (1966),[2] six on needles of *Pinus sylvestris* by Hayes (1965)[3] and seven on the roots of various crop

*The list of fungal species found by Hering on all four types of leaf litter are as follows (the numbers refer to the references given above); *Botrytis cinerea* (1, 2, 3, 4); *Paecilomyces farinosus* (2); *Gliomastix murorum* (2); *Cephalosporium* sp; *Verticillium lecanii*; *Aureobasidium pullulans* (2, 3, 4); *Cladosporium herbarum* (1, 2, 4); *Epicoccum nigrum* (1, 2, 4); *Penicillium frequentans* (2, 3); *P. thomii* (1, 2); *P. coeruleoviride*; *Trichoderma viride* (1, 2, 3, 4); *Mucor hiemalis* (1, 2, 3, 4); *M. rammanianus* (1, 2, 3, 4); Sterile 1785.

plants by Parkinson *et al.* (1963).[4] Among the commonest of these species are various Mucoraceae such as *Mucor hiemalis* or Hyphomycetes such as *Aureobasidium pullulans*, *Epicoccum nigrum*, *Cladosporium herbarum* and various species of *Trichoderma* and *Penicillium*. As Hudson (1968) pointed out, the definition of the role played by these 'generalist' micro-organisms within decomposer communities is a problem of particular interest.

The 'unit-community'

Plant resources occur as a series of discrete 'units' of variable size and origin. In the case of woody materials, for instance, the units may vary considerably in size from small twigs to large branches or stems (Whittaker & Woodwell 1968). The distribution of the twigs and branches in the litter layer of a woodland is nonrandom in space and time, dependent on the spatial and age distribution of the vegetation from which it originates (Healey & Swift 1971). The decomposer organisms associated specifically with wood decay will therefore have spatial and temporal distribution patterns determined partially by the resource distribution. A different type of resource, such as leaf litter, may, in temperate woodlands with only one or a few tree species, and a much more restricted season of fall, show much less variation in size and more homogeneity in distribution. In other areas, tropical forest for instance, the variation may be just as great as for wood. Within this resource determined pattern there is also a considerable extent of secondary spatial heterogeneity in the distribution of the microbes. Fig. 8.1 shows data derived from an isolation study of fungi from 10 cm long samples of wood taken from beech branches of variable length and between 2 and 5 cm in diameter. The branches were selected from the litter layer of a woodland by a 'nearest neighbour' sampling technique (Healey & Swift 1971). 56 species were isolated from the total sample of 32 branches. 15 isolation plates were made for each branch. The distribution of species between branches shows a modal species number of four with a range from one to nine (Fig. 8.1a).

Thus each individual branch has a community of micro-organisms of varying diversity, comprising several species of fungi plus bacterial and other microbial components. Such partitioning could presumably be demonstrated for other resource types such as roots, fruits, or leaves. Such communities may be termed '*unit-communities*' and regarded as having a functional integrity. As such the unit-community resembles an 'association'. However, as the following discussion will show, the degree of constancy of the unit community in species composition may be low, which is in direct contrast to the implication of the 'association'. It should rather be regarded as a spatial unit within the whole microbial community structure which is de-

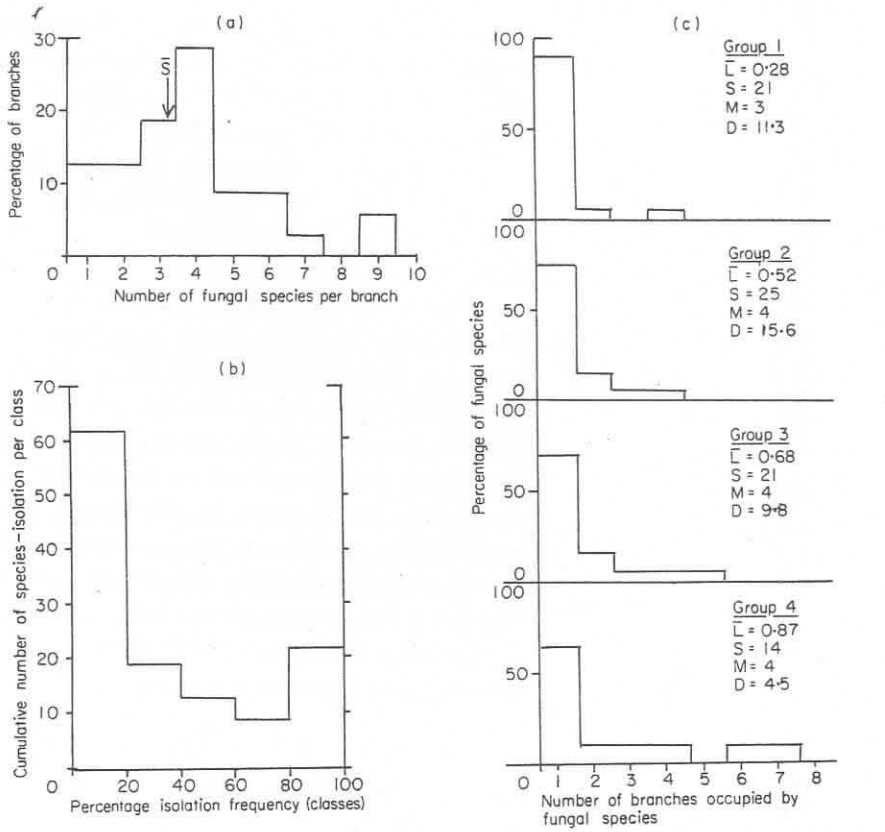

Figure 8.1. Distribution of species of fungi within a sample of branches of beech (*Fagus sylvatica* L.) taken from the litter layer of coppiced woodland. (a) Numbers of species isolated from each branch (Total number of branches, N=32; $\bar{S}$=Mean number of species per branch=3·9). (b) Distribution of species within branches (within unit-communities). For each of the 32 branches the frequency of isolation of each species was determined as the percentage occurrence on the (15) isolation plates for each branch. The species were grouped into frequency classes (X axis) and totalled for the full sample (Y axis). Thus for the full sample a total of 125 species isolations were made (=$\bar{S}$.N). The histogram thus gives a 'profile' of the species abundance pattern within an 'average' unit community branch. (c) Changes in the mycoflora during decomposition. Each histogram contains data for N/4=8 branches as sub-samples of the samples of (a) and (b). $\bar{L}$=Mean fraction of weight lost (compared with living beech wood on the basis of RD—see text); S=total number of fungal species from subsample; M=Modal number of fungal species per branch; D=diversity index=$1/\Sigma p_i^2$, where p_i=relative frequency of isolation of any species *i* (Simpson 1949; MacArthur 1972) in this case summed for all the species within each of the subsamples.

termined solely by the spatial, temporal and size class distribution of resource units. The unit-community provides a convenient basis for the analysis of community structure and function and will be the main concern of the remainder of this paper.

The number of microbial species within a unit-community may be relatively small. The data of Fig. 8.1a show a modal fungal species number of four. However, further examination of this wood decay data shows that a very considerable degree of variation exists *between* unit-communities. Two-thirds of the fungal species were isolated from only one of the branches. Only five fungi were isolated from five or more of the 32 branches; these included such RN types as *M. hiemalis* and *T. viride* and specialized wood decay (though not species specific) Basidiomycetes as *Stereum hirsutum*. The occurrence of regular associations between species was almost totally confined to that of the former two species. The major component of diversity in the fungal community of branch-wood is explained by partitioning between different species of resource or between units of the same resource. The features which may determine the partitioning of species between units are discussed in detail below; the question of the factors which determine the internal structure of the unit community are discussed in the next section.

THE INTERNAL STRUCTURE OF THE UNIT-COMMUNITY

Fig. 8.1b shows some aspects of the structure within the unit-community. The majority of species were isolated only infrequently and the second largest group of species were those that were isolated with high frequency (i.e. occurred on more than twelve out of fifteen plates) from the logs they inhabited. This distribution suggests that most of the microcommunities have single dominants associated with two or three rare species. Exceptions to this occurred in six of the 32 branches in which the two commonest RN species, *T. viride* and *M. hiemalis* were both isolated with high ($>50\%$) frequency. Thus in these cases alone something of a constant association can be said to occur. More will be said in relation to the role of these particular species later but on this evidence for wood-decay specific associations seem relatively rare. Only further work will reveal whether this is general, both in wood decay and for other resource types.

The co-existence of microbial species within unit-communities is dependent on the presence of a variety of niches which are determined by either chemical (substrate) factors or by factors of the physical environment. These factors determine how the capacities of microbes for decomposition are deployed.

Substrate affinities among decomposer micro-organisms

Plant materials, the primary resources of decomposer organisms, are complex both in their internal structure and their chemical composition. The structural complexity is due to the presence of different cell types and tissues within the resource. This may affect the distribution of the microflora in three ways: (1) The differing chemical composition of different cell types may have a selective effect on the microflora. (2) Different types of plant tissue create different physical environments again leading to differential effects on the microflora. (3) The differing chemical and physical nature of different tissues affect their palatibility to decomposer animals; the activity of these organisms may exert a strong selective and/or regulatory effect on the microflora. Only the first of these effects will be considered in this section.

The organic components of plant litter can conveniently be placed in three categories of differing significance to decomposer organisms; as sources of carbon and energy (*energy molecules*); as sources of elements other than carbon (*nutrient molecules*); or as molecules that have effects at relatively low concentrations either because they are essential to the growth of auxotrophic microbes or because they have an effect, stimulatory or inhibitory, on the activity of the microbes (*modifier molecules*). All three of these components may be distributed heterogeneously within primary resources and thus lead to spatial partitioning of the microflora.

Modifier molecules may have marked effects of this kind; many tannins and polyphenols which have an inhibitory effect on the activity of microbes may be localized in their distribution. For instance in wood they are in the highest concentration in the bark (periderm) and in the heartwood. This may be one of the features determining the existence of a distinct bark microflora (Bier 1963; Grosjean 1950). The suberins and cutins of external tissues also have selective effects on an invading microflora although ultimately they are metabolised as energy molecules (Martin & Juniper 1970). The distinction of bark and wood microfloras in woody tissues is also enhanced by the distribution of energy molecules such as sucrose or starch which have a storage or translocatory function in the plant. The distribution of these molecules is strongly correlated with that of living (parenchymatous) cells (Priestley 1962). The distribution of nutrient molecules, such as those containing N, also follows a similar pattern (Merrill & Cowling 1966). It is a feature of colonization by many wood decay organisms that they grow initially in the cambial and ray parenchyma. In some cases, e.g. the blue-stain fungi, growth may be limited to this area.

In most resource types the bulk of the energy molecules are found in the components of the cell wall. The structure of cell walls in different tissues

Table 8.2. Chemical composition of the cell walls of sycamore stem tissue, with particular reference to the polysaccharide components. Data re-calculated from Thornber & Northcote (1961a, b, 1962).

(a) Composition of different plant tissues (% dry weight)

	Outer Phloem	Inner Phloem	Cambium	Sapwood	Heartwood
Pectic substances	3·1	6·6	15·0	3·8	1·3
Hemicelluloses	21·3	25·8	45·0	31·5	31·4
α-cellulose	29·0	45·0	36·7	40·0	43·0
Lignin	46·9	22·6	2·5	25·3	24·3
Mean cell weight (mg)	—	—	15·3	157	171
Mean cell length (mm)	—	—	0·52	0·72	0·68

(b) Composition of different polysaccharide fractions in sapwood (% dry weight)

	Hemicellulose fractions				
	Xylan	Glucomannan	Hemicellulose I	Hemicellulose II	α-cellulose
Glucose	18·7	20·4	8·9	30·4	95·0
Galactose	0·0	0·0	2·8	0·0	0·0
Arabinose	Trace	0·0	1·6	0·0	0·1
Xylose	69·2	33·2	73·8	15·0	1·2
Mannose	0·0	39·8	0·0	51·0	3·5
Uronic anhydride	12·6	3·9	11·4	3·2	0·0
Methylgluronic anh.	12·2	0·0	0·0	0·0	0·0
Percentage of total fraction	48	2	42	8	—

of plant resources may differ considerably (Table 8.2a). Moreover, modern studies on the composition and structure of plant cell walls have revealed an extremely high degree of complexity at the molecular level. This exists not only in the internal complexity of many of the individual polysaccharides (Table 8.2b) but also in the physical arrangement and intercomponent binding of the polymers in the wall (Northcote 1972). Cellular differentiation and the deposition of additional polysaccharide and lignin, with a corresponding increase in the density of the wall (Table 8.2a) adds further elements of complexity.

The heterogeneity of distribution of cell wall types within plant resources creates the potential for a considerable extent of partitioning of the microflora on the basis of differing nutritional capacities and preferences. To what extent may this be realized among the decomposer microflora? Only a small group of organisms, the white-rot wood decay Hymenomycetes is capable of totally degrading this complex cell-wall material (e.g. see Findlay 1940). In order to do this they must possess a formidable array of enzymes; the polysaccharases which catalyse the depolymerization of cell wall components are highly specific in their action. So much so indeed that Albersheim *et al.* (1969) in a review of the enzymatic breakdown of cell wall components remarked that 'in all biology there is no molecular interaction more specific ... than the recognition of saccharides by proteins'. This specificity relates to the constituent sugars, to the position of the glycosidic bond(s) (e.g. 1—2, 1—3, 1—4, 1—6 etc.), to the steric relationship of the monomers (α or β bonds) and finally to the presence or absence of side branches or substituted groups (Reese 1968). This is illustrated in Table 8.3 for a brown-rot fungus *Coniophora cerebella* for which more depolymerizing enzymes have been positively identified than for any other decomposer microbe (King 1966). It should be noted that the extent of definition of the enzyme system

Table 8.3. Depolymerizing enzymes detected in cultural filtrates of *Coniophora cerebella* (King 1966; King & Fuller 1968).

Polysaccharide	Bond attacked	Polysaccharase	Glycosidase
Cellulose	Gβ1—4G	+	+
Laminarin	Gβ1—3G	+	
Xylan	Xβ1—4X	+	+
Glucomannan	Gβ1—4G	+	
	Gβ1—4M	+	
	Mβ1—4G	+	
Arabinogalactan	Galβ1—3Gal	+	
	Galβ1—6Gal	+	
Pectin	GalUα1—4GalU	+	

G=Glucose; X=Xylose; M=Mannose; Gal=Galactose; Gal U=Galacturonic Acid.

is dependent on the availability of substrate molecules to determine their action and it is the absence of the latter that is probably the main limitation to our description of the enzymatic capacities of decomposer organisms.

The most intensively studied of the polysaccharide-degrading systems, the cellulose enzymes of fungi, has revealed further levels of complexity. The catabolism of cellulase involves the participation of at least four different enzymes C_1 ('hydrocellulase'), endo- and exo-β-glucanase (Cx components), and β-glycosidase, each catalysing a different step in the depolymerization of the molecule and its assimilation into the metabolic pool of the fungus. It is probable that most of the other polysaccharides require at least two of these enzyme types, the endo-polysaccharase and the glycosidase, for their extracellular catabolism although this has been demonstrated for only a few polymers (Table 8.3). The enzymatic degradation of lignin is not well understood but it is clear that several enzymic steps must be implicated in view of the variety of monomers and inter-monomeric bonds (Kirk 1971).

Most of the available data on the subject of the enzymatic capacity of decomposer micro-organisms relates to only a limited range of activities commonly including some measure of cellulolytic, pectinolytic and ligninolytic ability. Furthermore, the usual methods of testing do not necessarily correlate with the abilities of the organism in relation to the decomposition of plant tissues. For instance *Trichoderma viride* has been used in the laboratory as a producer of some of the most active of cellulase systems (Selby 1968). However, when inoculated on to plant materials such as oak leaves (Hering 1967) no cellulose breakdown was demonstrable although breakdown of hemicellulose components was detected. Three possible reasons exist for this type of conflicting evidence:

(1) The interactive effects of the cell wall components. It is known that the presence of lignin in the cell wall can have a 'masking' effect and slow the rate at which cellulose and other polysaccharides are degraded (Bailey *et al.* 1968). This emphasizes the multiple-enzyme nature of the degradative systems; the possession of a single enzyme, even one as fundamental as a cellulase, does not guarantee the decomposition capacity of the organism.

(2) The use of misleading tests in the laboratory. In the case of *T. viride* the existence of the C_1 component of the cellulase complex is well established. However, much of the laboratory screening for cellulolytic ability in micro-organisms by ecologists has employed the use of degraded forms of cellulose such as filter paper. Whilst this establishes the capacity for polysaccharase production, the activity of the organism on intact cell walls may depend on the production of C_1 fractions. On the other hand it should be noted that the absence of C_1 does not necessarily mean that an organism will be unable to benefit from the capacity to produce Cx. Selby (1968) has demonstrated how the C_1 and Cx components from two different organisms

may combine in the degradation of crystalline cellulose. Similar criticisms may apply to the use of the Bavendamm Reaction as a test for ligninolytic activity (Henderson 1960). This test involves distinguishing the capacity to colourize by oxidative action phenolic compounds such as gallic or tannic acids. The polyphenol oxidase enzymes involved in the oxidative reactions probably do not play any direct role in lignin depolymerization.

(3) The existence of genetic variation. The same species of fungus may embrace variants differing in one or more of these enzyme capacities. This feature may well explain some of the apparently contradictory reports on enzymic capacities found in the literature (e.g. see Hudson 1968).

For these reasons it is difficult at this stage to make any substantial generalizations concerning the distribution of enzymic capacities within the decomposer microflora. Two features do emerge from recent work however; firstly that as more investigation is carried out the more widely distributed these enzymic capacities are shown to be. For instance the earlier suggestions that there was a general taxonomic correlation between the absence of cellulolytic ability in the Phycomycetes and the confining of ligninolytic activity to the Basidiomycetes has now been broken down by an increasing number of exceptions (e.g. Park, Chapter 3; Henderson 1960). Secondly that there is considerable variation in the combination of capacities exhibited by any one organism. Table 8.4 illustrates this for a sample of litter and soil fungi from Tundra (Flanagan & Scarborough 1974). It was possible to subdivide the 35 species tested into 13 groups varying from those combining all activities to those with none. This implies a very considerable potential difference in the 'biochemical strategy' for the obtaining of energy and carbon on the part of decomposer fungi.

Table 8.4. Degradative capacities of fungi isolated from soil or from debris of *Eriophorum angustifolium* or *Carex aquatilis* at Point Barrow, Alaska (Flanagan & Scarborough 1974).

Total species tested	35
(1) Individual Capacities	Number of species
Starch Hydrolysis	30
Pectin Hydrolysis	27
Cellulose Hydrolysis	7
Gallic Acid Coloration	14
Humic Acid Clearing	8
(2) Combinations of Capacities	
Total possible combinations	32
Number combinations observed	13

Table 8.5. The utilization of polymeric or simple C sources by bacterial isolates from two species of leaf litter (Hissett & Gray 1974).

	Percentage of isolates utilizing C source	
Source of Isolates	Oak	Ash
Pectin	1	0
Xylan	6	5
Cellobiose	36	45
Glucose	72	63
Xylose	76	69
Chitin	0	2
Glucosamine	3	36
Vanillic Acid	0	1

The capacity for depolymerization is probably less widespread in the bacteria and actinomycetes than in the fungi (Table 8.5). However, considerable variation does exist in the combinations of molecules that can be used by these decomposer microbes as is shown in the patterns of utilization of C and N sources by an actinomycete flora illustrated in Fig. 8.2. The number of different combinations of utilization was again considerable in these examples.

The potential for interaction of a synergistic kind between decomposers of differing biochemical potential has been mentioned above in connection

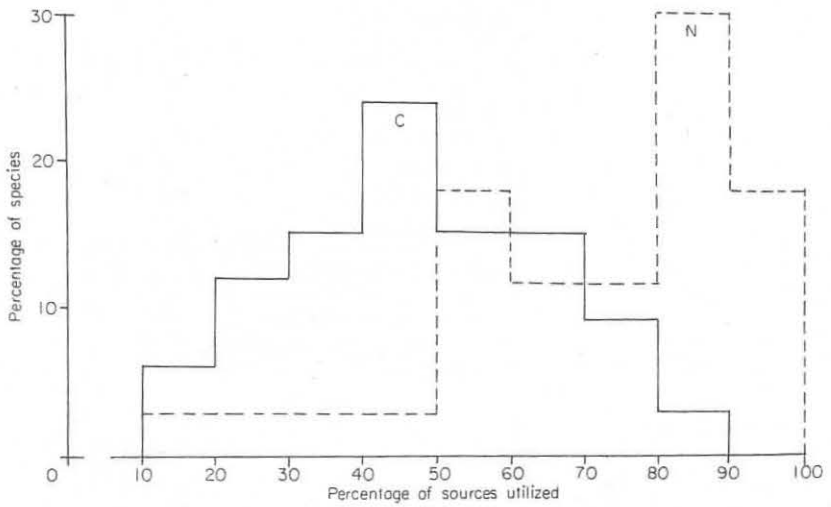

Figure 8.2. The proportion of simple carbon sources (n=22) and nitrogen sources (n=25) utilized by 33 species-groups of actinomycetes isolated from a woodland humus soil (Szabo 1974).

with depolymerizing reactions. A considerable extent of this may also exist through other biochemical functions. It is now accepted that the regulation of many depolymerizing enzymes probably operates through a system of catabolite repression (Lewis 1973). This has been demonstrated clearly for the cellulase system of *Myrothecium verrucaria* by Hulme & Stranks (1971) who demonstrated that concentrations above any but negligible levels of glucose, cellobiose, or other simple carbohydrates will repress the production of cellulase enzymes.

The activity of extracellular enzymes are outside the normal regulatory mechanisms of the cell. Thus it is entirely possible for the production of sugars to exceed the rate at which a cellulolytic organism can absorb and use them. This would be regulated in a mono-culture situation by the switching on and off of the cellulase production by the catabolite repression mechanism. However, the presence of other organisms utilizing the sugars may result in the continuing production of the polysaccharase. Garrett (1963) defined noncellulolytic organisms which grow at the expense of cellulosic substrates in this way as 'secondary sugar fungi'. There have been a number of demonstrations of the capacity of these organisms to benefit from the activity of cellulose decomposers (Tribe 1966; Hedger & Hudson 1974) and of the stimulation of the rate of cellulose breakdown by their synergistic interaction (Enebo 1963).

Clearly the potential for co-existence in a noncompetitive manner of microbial species by the adoption of differing patterns of substrate utilisation is considerable. It is also possible that within different unit-communities a species may adopt a different biochemical role, i.e. an organism that is cellulolytic in one community may act as a 'sugar-fungus' in another. It is probable that the interaction between species within unit-communities are symbiotic rather than antagonistic in nature, at least during the early stages of decomposition before nutrient sources become limiting. This may contrast with the low nutrient situation of soil environments where antagonistic interactions probably predominate (Park 1960). The potential for niche diversity created by substrate factors is broader than the above discussion implies for it has been confined to the carbon and energy obtainable from cell walls. The other constituents of primary resources (including nutrient molecules), add further substrate diversity as do the components of the secondary resources which become available during the later stages of decomposition. The dead tissues of fungi, bacteria and soil animals contain a variety of energy molecules in bulk which are not found in plant cells. For instance chitin is found in the cell walls of fungi and in the exoskeleton of many arthropods; the cell walls of all the microbes contain a range of other polysaccharides not found in plants; the storage polysaccharides of both animals and microbes are different from those of plants; the extracellu-

lar products of decomposition, including the components of the humus, also provide a potential food resource for the decomposer community.

THE INFLUENCE OF THE PHYSICAL ENVIRONMENT

The complexity of the features of the physical environment at the scale of the microhabitat and the selective effect that many of the features have on microbes in the soil have been reviewed in detail by Griffin (1972). Much less is known of the micro-environments of plant litter, and very little indeed in relation to the distribution of species components of the decomposer microflora (Williams & Gray 1974). Webster (1956) found that the diversity and composition of the fungal flora on stems of cocksfoot showed significant differences between internodes. Whilst nutritional factors played some role in this the moisture regime was demonstrated to be one of the major determinants (Webster & Dix 1960). Similar stratification of moisture levels within decomposing plant tissues, and associated differences in the partial pressures of O_2 and CO_2, may result in the spatial segregation of different components of the microflora. For instance bacteria may dominate waterlogged parts whereas fungi predominate in the more aerobic zones. This could occur where litter is in contact with very wet soils.

The definition of micro-environmental features of this kind within plant litters has been given little attention by microbiologists. The application of direct observation methods such as soil sections to the study of the litter horizons (Anderson 1971), has revealed the topographic complexity of these layers and indicates the potential diversity of physical environments within them. In particular the distinction between 'surface colonizers' and colonizers of the interior of plant resources which has been made in a number of studies (e.g. Kendrick & Burges 1962; Hogg & Hudson 1966) may well relate to adaptations to different physical environments.

Niche diversity and species diversity

In the preceeding discussion I have suggested that the microflora of decomposer habitats may exist in a mosaic structure, exhibiting patterns of distribution at varying scales which are determined by the spatial distribution of the primary resources and their components. Most of this pattern is undescribed and these suggestions are as yet hypothetical. The structure of experimental investigation has not been designed to describe it and such evidence as exists is incidental in nature (e.g. Fig. 8.1). In Fig. 8.3 the proposed structure is summarized in diagrammatic form. Features of structural

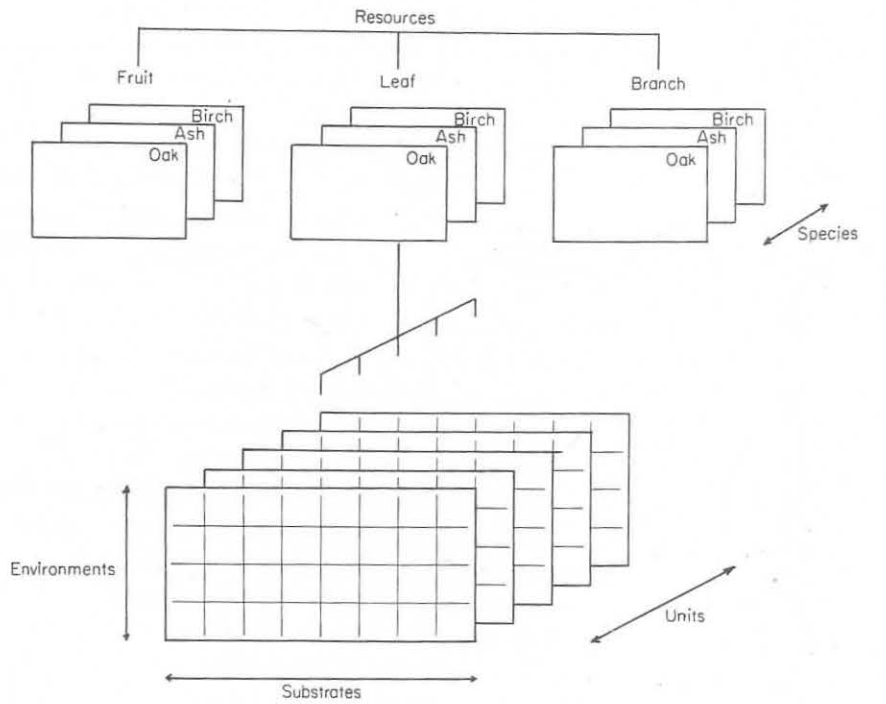

Figure 8.3. Diagrammatic illustration of the spatial partitioning of the decomposer microflora. Organisms occupying different boxes are regarded as existing noncompetitively (except possibly during colonization, see p. 213) those separated by lines may enter into competitive interaction if there is any significant reduction in the within-box area and heterogeneity (see also Fig. 8.6). Note that there is amplification of scale in the diagram between the resource and unit levels.

complexity additional to those illustrated are derived from primary resources such as roots and dead standing material which are spatially separated from the litter horizon, and from size variation in the primary resources. Any increase in the variety of the primary resources increases the heterogeneity, as does the variety of secondary resources. A considerable proportion of the partitioning of the microbial community is pictured as noncompetitive in nature. Organisms in different unit-communities are spatially separated (Fig. 8.3) and often may be separated in time as well, particularly in resources such as branch wood, where colonization may occur throughout the year (see below).

Within the unit-community the ability to co-exist depends on the continuing variety of available substrates and the complexity of micro-environments. The fundamental niches are largely defined by these two sets of parameters. Any decrease in the variety, quantity and accessibility of substrates and in the variety of micro-environments will lead to overlap in

realized niches and an increase in competition between the micro-organisms occupying them. The development of this situation during the decomposition of a resource unit is discussed below.

A further prediction may be made concerning the niche structure of microbial communities—the existence of a large number of *equivalent species*. Within different units of the same resource the potential exists, because of their spatial and temporal discreteness, for extremely similar functional niches to be occupied by different species. The described structure of the community of beech wood is suggestive of this. It is possible to hypothesize that a Basidiomycete such as *Coriolus versicolor* in branch A and *Stereum hirsutum* in branch B occupy niches which are essentially definable by the same parameters e.g. cellulose, hemicellulose and lignin degrading capacity, tolerance of low O_2 and high CO_2 concentrations, demand for moisture contents above fibre saturation point. On large branches the two species may be found within the same unit; the similarity of niches is underlined by their spatial separation, often with the formation of interactive 'zone-lines' (Swift 1976). The explanation for the coexistence of such ecologically equivalent species probably lies in the circumstances of colonization of the resources. This may be a highly competitive process (e.g. see Rishbeth 1951) or the variety of successful species may be explained by the variety of colonization patterns available to micro-organisms.

I have suggested that a repeating mosaic of spatial heterogeneity determines the nature of the microbial community which is characteristic of any particular macrohabitat. Differences in the structure of this niche space are the factors which determine the differences in the diversity, composition, and structure of the microbial communities of different vegetation and soil types. Differences of this kind have been demonstrated in soil types both of close relationship (Christensen 1969) and of extreme difference (Sundman 1970). Attempts have only rarely been made to correlate these differences in microfloras with anything other than gross features of difference at the macrohabitat level and this is rarely informative. However, a factor which may prove useful in exploring the basis of such contrasts is the nature and distribution patterns of the primary resources within the habitat. The pattern of distribution of unit-communities may be a fundamental feature of community structure that is determined by the resource distribution.

Changes in community structure with time

The composition and structure of biological communities may be subject to change during the course of time. Such changes may be directional and

permanent or they may be cyclical, involving not permanent change in one direction but a regeneration of structure in response to a fluctuating, and often seasonal, environment (Park 1968). Changes of both types are discernible within the decomposer microflora and it is worth considering what factors are involved in directing these changes in the light of the discussion above.

SUCCESSIONAL CHANGE

Successional changes in the vegetation of an area towards the establishment of a climax community bring about progressive changes in the physical and chemical environments which in their turn exert selective effects on the heterotrophic component of the community. Changes in the composition of the plant community have direct effects on the component of the microflora which is symbiotic with the plants. The RS component of the saprotrophic microflora will be similarly subjected to changing selection pressures. Thus increasing species diversity in the vegetation will lead to increased diversity in the plant-symbiotic and RS saprotrophic microflora. The increasing variety of the primary resources entering the decomposer system and the progressive accumulation of organic matter within the system will increase the amount and variety of substrates and the heterogeneity of the micro-environments available to the microflora. Thus it can be predicted that the RN microflora will also increase in diversity during the development of the primary macrosere.

Pugh (1962) has shown changes in fungal species composition and increases in species diversity during the development of vegetation on coastal muds and Brown (1958) has demonstrated the same for sand dunes but in general very little information is available on microbial successions of this kind. Hayes (1965) commented on the striking differences in the number of species isolated in his study of pine needle fungi in comparison to those found by other workers. He suggested that the differences in species number might reflect the differing ages and maturity of the forests in question. The effects on microbial diversity of the diversion of the primary sere by factors such as fire and cultivation has yet to be explored in a comprehensive manner by microbiologists but the indications are that such peturbations result in a decline in species diversity and a change in species composition (e.g. see Widden & Parkinson 1974).

Whilst the seral development of the decomposer microflora has not received a great deal of attention by microbial ecologists the cyclical changes in microbial community structure have been a favoured subject for study and speculation.

CYCLIC CHANGE

The progressive decomposition of a resource unit breaks down the niche structure that I have suggested exists within it. Microbial catabolism depletes the primary resource of both the amounts and diversity of substrates, although the production of secondary resources may to a certain extent compensate for the latter. The physical character of the material is altered by the 'skeletonizing' effect of microbial decomposition and even more drastically by the comminutive activities of soil animals. This results in the complete restructuring of the physical environment at the microhabitat level. It is probable that the net effect is to increase the diversity of such micro-environments as the soil condition is approached. These changes in niche structure are not confined to the within-unit level; as decay procedes so both the physical and the chemical distinction between different primary resources declines so that within the humic materials (the *terminal resources* of decomposition) the origin of the components among the primary resources may be difficult to determine.

It has long been realized that such changes in the resources would have a profound effect on the inhabitant microflora. Garrett (1956, 1963) has pictured a succession of microbes progressively adapted to the changing chemical composition of the resource. Changes in the composition of the microflora during decomposition have been demonstrated for a variety of resource types and have been well reviewed by Hudson (1968) and others. The community change involved is essentially a cyclic one when considered from the scale of the decomposer habitat as a whole. A species which becomes inactive in a particular microhabitat survives by the re-colonization of a fresh resource; these microbes therefore exhibit behaviour typical of 'fugitive species' as characterized by MacArthur & Wilson (1967). The highly efficient dispersal methods shown by many of them is also characteristic of this pattern of colonization. As long as the supply of that resource is maintained, without change in its nature or amount, then the 'cycle' of each species can be maintained. Such changes are thus not directional or permanent except at the scale of individual units or microhabitats. Such a cycle will involve successive phases of colonization, exploitation, dispersal and re-colonization of the resource (Fig. 8.6). If a change in the resource supply does take place then the cycles will be broken and permanent directional change may occur. A number of the features of this type of cyclic change are reviewed here in relation to the illumination they cast on the postulated structure of microbial communities.

Changes in species diversity

An illustration of change in species diversity during progressive decomposition is given by the sample of decayed beech branches referred to earlier. The extent of decomposition of branch wood can be determined by measuring its relative density (RD) and comparing it with that of living wood (Healey & Swift 1971). The beech sample was found to show decay states ranging from 81% to 10% of the RD of undecayed branches. For further analysis the branches were grouped in four classes of equal size on the basis of consistency of state of decay. The data in Fig. 8.1c show that some quite marked differences in the structure of the microbial communities could be observed as decay progressed. The diversity of the macrocommunity (that of the total of branches in each of the four samples) decreased markedly in the terminal stages of decay. However, the size of the unit-communities remained constant at an average of four species per branch. The explanation for this apparent contradiction lies in the histograms of Fig. 8.1c. It is in the terminal stages of decay that the more frequent species, such as the *T. viride*/*M. hiemalis* association appear. Thus the effect of progressive decay is to bring about a decrease in diversity and an increase in homogeneity of species composition between different unit-communities.

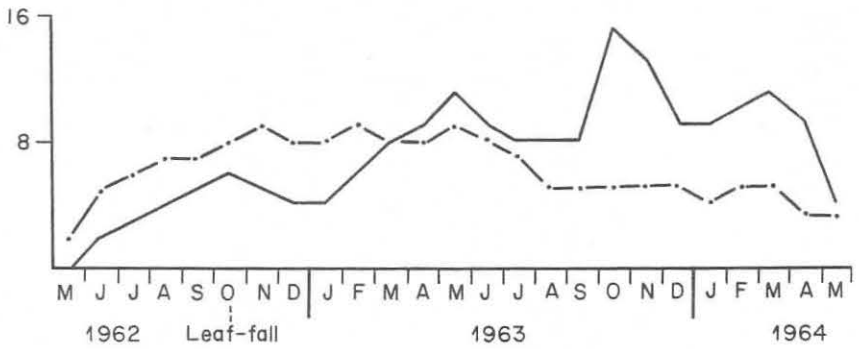

Figure 8.4. Variation in the number of species of micro-fungi recorded from monthly samples of twenty leaves of beech (*Fagus sylvatica L*). The leaves were placed in wire cages in the litter layer under a beech tree in 1962. The numbers of species recorded by direct observation are shown by the continuous line; the numbers of species isolated onto Potato-Dextrose Agar are shown by the broken line. Reprinted with permission from Hogg & Hudson (1966).

A similar decline in diversity is illustrated in Fig. 8.4 which is taken from a study by Hogg & Hudson (1966) of the succession of fungi on beech leaves. The number of species as determined by isolation techniques again shows a decline in the latter stages of decay. Note, however, the discrepancy between these results and those found by direct observation of fruiting.

If this decline in species diversity is a general feature then we should

Table 8.6. The numbers of species of micro-organisms isolated from leaf litter and different horizons of soil.*1 In the case of bacteria and actinomycetes 'species' are groups determined as defined in the respective papers.*2 The definition of soil horizons and the methods used to isolate organisms differed in the different studies so no vertical comparison of the data should be made.

Organisms	Dominant Litter Types	*2Litter	Humus	Soil	Reference
Fungi	*Eucalyptus maculata*	33	25	75	Eicker (1973)
Fungi	*Pinus strobus*,				
Fungi	*Acer saccharum*,				
	Ulmus americana	59	30	30	Widden & Parkinson (1973)
	Fraxinus pennsylvanica,				
	Quercus bicolor	161	96	—	Novack & Whittingham (1968)
Bacteria*1	*Quercus robur*				
	Fraxinus excelsior	12	11	10	Hissett & Gray (1974)
Actinomycetes*1	*Quercus robur*				
	Fraxinus excelsior	91	126	130	Williams *et al.* (1969)

expect to find significant differences between the number of species of fungi found in the successive horizons of soil. Table 8.6 records the results of a number of studies contrasting the species of micro-organisms isolated from leaf litter, humus, and mineral horizons of soil. The examples were chosen on the basis of internal consistency, i.e. the same workers using comparable methods at the same time on the same site. The decline in fungal diversity between litter and humus is confirmed although the increase in species number in the mineral horizon in the first example shows an interesting deviation from the general pattern. Further examples of declining diversity with depth have been shown for a variety of soils by Wicklow & Whittingham (1974).

An interesting feature of these results is the contrast in the behaviour of the fungi and the other microbial groups. Whilst the fungal diversity is generally lower in the organic and mineral horizons than in the litter layer that of the actinomycetes is considerably enhanced. The same may apply to the bacteria for Hissett & Gray comment that the heterogeneity of the humus layer bacteria was even greater than their results indicate because of a large proportion (56%) of isolates which did not associate with any of their defined groups. This is probably related to the much smaller size unit of the bacterial colony than the functional unit of the fungi which is the apical region of the hyphae. This probably confers great responsiveness to the developing complexity of the physical environment at the micro scale during the establishment of the particulate structure of soil.

Changes in species composition

The fact of change in species diversity and in particular that of change in the number of species implies that the species composition of decomposer communities varies as decomposition proceeds. This 'succession' involves the addition of new species to the community at specific times during the process of decomposition and the extinction of others at subsequent times. The demonstration of these events is by no means simple as the isolation data for two selected species from Hering's (1965) study of Ash leaf litter illustrates (Fig. 8.5). Both species are shown to be present throughout the decay period but show considerable fluctuation in the frequency of their isolation. The periodic absence of the species from the isolation plates can be attributed to a number of possible causes. (1) The sample taken at that particular time lacked any leaves with that particular fungus present, i.e. this is an effect of the distribution of species between 'units' of the resource. (2) Environmental factors may have differentially eliminated the species over this period but subsequent reinoculation re-established it. (3) The fungus

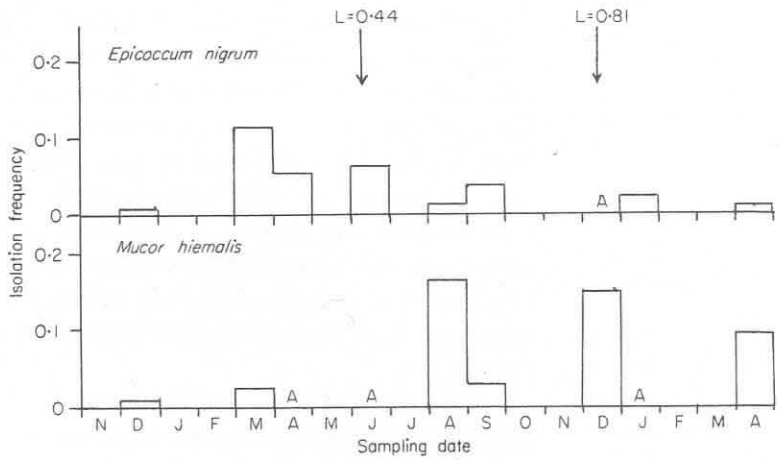

Figure 8.5. Contrasted patterns of change in relative abundance of two species of fungi during the decomposition of Ash leaves. Data redrawn from Hering (1965), Table 3, p. 396. Isolation frequency = Ci/Ct, where Ci = number of colonies of species *i* and Ct = total number of colonies for all species; A = species absent; L = fraction of weight lost by decomposition.

was present but failed to appear on the isolation plates, possibly because of competitive effects of other fungi on the agar medium.

However, despite the fluctuations of abundance from month to month a contrast in pattern between these fungi can be discerned. *Epicoccum nigrum* shows an early maximum in relative abundance which then declines whilst *Mucor hiemalis* shows a complementary pattern. The periods of high isolation frequency may be interpreted as representing periods of exploitation of the resource. The periods of low relative abundance may represent stages of either inoculation and colonization or terminal resting phases such as chlamydospores or sclerotia. In most recent work washing techniques have been employed to try and rid the resource of spores prior to plating-out so that it is probably reasonable to assume that isolation frequencies are proportional to present or past mycelial abundance. The direct observation of the organism fruiting on the plant material (Fig. 8.4) may confirm previous exploitative activity but it cannot establish the period or extent for which this activity has taken place.

Despite these difficulties of interpretation it has proved possible to build up a picture of the 'successions' of fungal presence and activity on a number of primary resources. Hudson (1968) has reviewed these studies and suggested that for many types of leaf and herbaceous litters some general correspondence of pattern could be discerned in the observed changes. The primary flora, originating on the senescent standing leaf, was comprised of weak parasites which are of course highly resource specific, and a number of RN

'*primary saprophytes*'. Some of these originate from a persistent phase in the phylloplane of the living leaf and could therefore also be symbiotic. After litter fall this RN component, which includes such species as *Cladosporium herbarum* and *Epicoccum nigrum*, persists and increases in abundance. The RS component is added to by the appearance of saprophytic species whilst the parasitic component disappears. Maximum diversity coincides with the upsurge of a group of '*secondary saprophytes*' most of which are RN components of the 'typical soil flora'. These include such genera as *Penicillium*, *Trichoderma* and *Mucor* as well as the litter inhabiting Basidiomycetes. This community eventually replaces the earlier 'primary' flora. These changes are illustrated in Fig. 8.6.

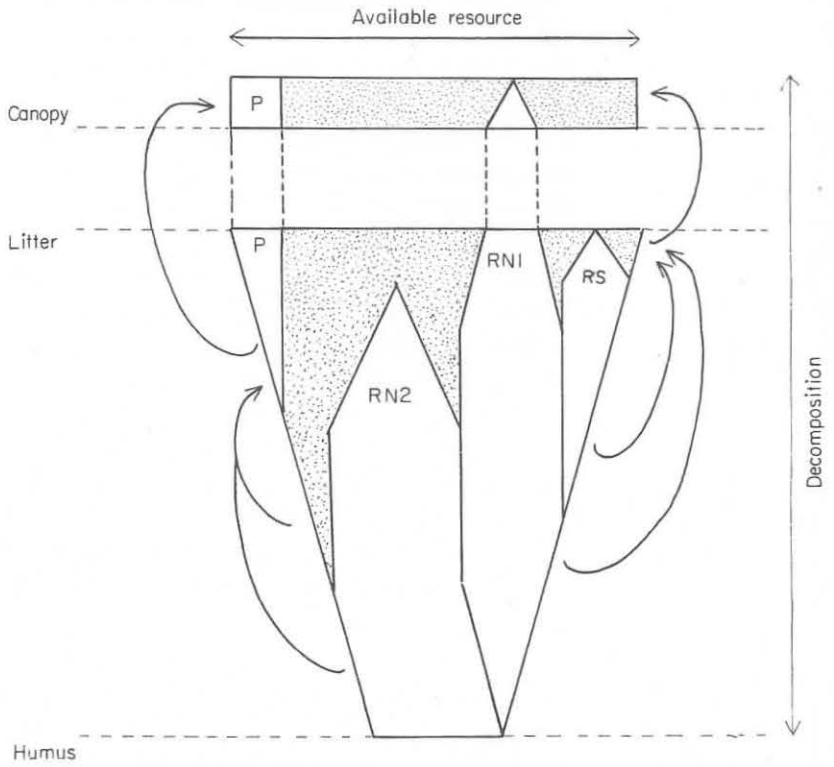

Figure 8.6. Diagrammatic representation of the cyclic changes in fungal community structure on an 'average' resource unit. Unstippled areas represent the extent of occupation of available resource by fungi. The arrows represent the dispersal of fungal propagules. P = parasitic species; RS = resource-specific saprophytes; RN_1 = primary resource-nonspecific species; RN_2 = secondary resource-nonspecific species. Note that this 'succession' may be diverted if the resource is consumed by soil animals with consequent changes in pattern of colonization, chemical composition of the resource and particle size.

INTERPRETATION OF THE CHANGES IN DIVERSITY AND COMPOSITION

Succession in relation to the concept of the unit-community

In all the studies reviewed by Hudson, as with the beech-wood 'succession' reported here, the described changes in species composition relate to multiple-unit samples taken from the resource type in question; in no case is it possible to describe the changes that may occur *within* individual units or of the possible differences in pattern that may exist *between* different units. If it is accepted that it is at the unit-community level that the most significant interaction of species occurs, then it is clear that attempts to categorize species ecologically in terms of the times at which they occur in 'successions' which are based on analysis is of the macrocommunity may result in the comparison of organisms which have a markedly different significance in terms of the development of their own unit-community. To put it another way; whilst the 'succession' is conceived at a microhabitat level, its description is usually based on observations at a much greater scale. The one major exception to this has been the coprophilous 'succession' where the fruiting sequence on the same faecal pellet has commonly been observed through protracted periods of time. In this case it has clearly been demonstrated by Harper & Webster (1964) that all the member species of the unit-community are present from the initiation of the decay period; the sequence of fruiting observed is explicable in terms of differing physiological behaviour among the members of the unit community. Whilst the coprophilous 'succession' may be regarded as a special case—it is in effect a secondary or divergent succession of the sequence on the primary resource—the findings of Harper & Webster do urge caution in assuming the reality of sequences based on comparisons of samples of greater than single-unit size.

The nature of the communities at different stages of decomposition

Changes in species composition and diversity may imply changes in the functional attributes of the community and its component members. Garrett (1951, 1956, 1963) proposed that there was a sequence corresponding with the dominance of different 'substrate groups' of fungi; sugar fungi followed by cellulolytic fungi followed by ligninolytic fungi. He also recognized that sugar organisms might coexist with cellulose decomposers by benefiting from the excess sugars produced by extra-cellular enzyme activity. As mentioned earlier it has become increasingly difficult to define these simple substrate groups with any clarity. The correlation of organism sequence with

Table 8.7. Pattern of change in chemical composition of various resources during the initial stages of decomposition. (a) Comparison of the fractional loss in the components. (b) Comparison of the fractional contribution of each component to the total weight loss. + = apparent increase in component weight in comparison to original. Initial decay periods, 1 = 27 days, 2 = 66 days. Data re-calculated from Tenney & Waksman (1929).

	(a) Fraction of original component lost				(b) Fraction of total weight loss			
	Corn stalk[1]	Rye straw[2]	Oak leaf[2]	Alfalfa[1]	Corn stalk[1]	Rye straw[2]	Oak leaf[2]	Alfalfa[1]
Dry matter	0·36	0·17	0·22	0·30	—	—	—	—
Ether-soluble	0·30	0·53	0·26	—	0·02	0·06	0·04	—
Cold H_2O soluble	0·80	0·61	0·81	0·30	0·23	0·16	0·30	0·12
Hot H_2O soluble	0·55	+	0·46	0·26	0·05	+	0·12	0·04
Hemicellulose	0·31	0·22	0·27	0·49	0·20	0·27	0·16	0·14
Cellulose	0·44	0·24	0·34	0·41	0·35	0·54	0·21	0·36
Lignin	+	+	+	0·02	+	+	+	0·01

functional sequence is also unclear. Recently Pugh *et al.* (1972) have pointed out that the majority of Hudson's 'primary saprophytes' (RN1, Fig. 8.6), that are present on the leaf from early senescence possess some measure of cellulolytic and other depolymerizing activities. The most telling evidence against a nutritional interpretation, however, rests on the absence of correlation with the pattern of chemical change in the resource. One of the features that led to the derivation of the substrate group hypothesis was the observation that the initial rates of loss of different components could be clearly ranked; sugar>hemicellulose>cellulose>lignin. This feature, which has been discussed in some detail by Minderman (1968), can however be misleading in the present context. There is surprisingly little detailed data from which the comparison can be made but it does generally hold. This is shown in Table 8.7a for the classical studies of Tenney & Waksman (1929). Here three out of the four types of resource show a much higher fractional rate loss in the water-soluble (sugar) components than in the cell wall polysaccharides; the breakdown of lignin in all cases is negligible or undetectable. However, if the same data are recalculated (Table 8.7b) to show the proportional contribution to total weight loss of the weight lost in each chemical fraction, then it can be seen that the absolute quantities of cell-wall polysaccharides metabolized during this initial period exceeds that of the sugars. Putting it another way, the amount of initial microbial production attributable to energy from cell wall polymers is greater than that from sugars, particularly when it is remembered that a considerable fraction of the latter is probably lost due to physical leaching rather than microbial metabolism.

Thus there seems no reason to suppose that the functional interrelationships within the unit-community, or indeed the macrocommunity, change significantly with time, at least during the early stages of decay. The predominance of some niche determinants may change and with it the community structure but the internal functional structure will remain fundamentally similar and the interaction of polysaccharolytic and sugar-utilizing functions will be a common feature rather than the predominance of one or other feature.

The factors determining the appearance of new species

If the 'successional' features that have been described for the macrocommunity apply to the unit-community, namely that there is a significant time sequence in the addition of new species to the unit-community, then the elucidation of the factors that determine these differences in time of colonization becomes a feature of considerable interest. In considering this question

it is useful to distinguish between factors concerned with the process of *inoculation* and those determining *colonization*.

Success in occupation will depend in the first instance on the presence of propagules of the organism at the surface of the resource. It is noteworthy that the RN component of Hudson's primary microflora contains many organisms, such as *Cladosporium herbarum*, that are common members of the phylloplane flora of the living leaf, or in some cases may even be mildly parasitic in relation to senescing leaves, e.g. *Botrytis cinerea*, *Aureobasidium pullulans* (Pugh & Buckley 1971). The ability to persist in the specialized habitat of the phylloplane thus contributes to the decomposer potential of these organisms. They may be contrasted with Hudson's secondary RN fungi, which are less commonly found in the phylloplane or as major components of the air-spora than the primary saprophytes (Gregory 1973). It is possible to also contrast these secondary species with the other component of the primary group, the RS species, in terms of their differing modes of dispersal. The Ascomycete members of the latter group discharge their spores by violent means in to the air; most of the former group, *Penicillium* spp. and the Mucoraceae for instance, are reliant on passive means of dispersal. In many cases this may most commonly mean the carriage of the spores in soil water and on (or in) the bodies of soil animals. Thus the dispersal of this group will be over distances on a microscale largely within the litter and soil milieu as contrasted with the wider-scale aerial dispersal of the primary saprophytes. It is noteworthy that the commonest time of fruiting in many of the leaf-inhabiting ascomycetes is in the late summer and autumn, coinciding with the time of leaf senescence and litter fall.

It is clear that the pattern of spore discharge and dispersal and the timing and location of spore deposition may be an important factor in the establishment stage of community structure. Little can be said in detail at present but this is an area readily accessible to experimental investigation.

The presence of spores or other propagules on the surface of a resource does not necessarily ensure success. Selective effects may be imposed on the microflora at the penetration stage of colonization. On senescent or dead tissues these effects will not be as manifold and complex as they are known to be in the resistance of living plants to invasion by potential pathogens but some features in common may be expected. Thus the presence of cuticular materials resistant to enzymic breakdown or containing fractions that have fungistatic properties (Martin & Juniper 1972) may delay the penetration of some species. Further restriction may be imposed by selectively toxic 'plant protection' chemicals in the senescent tissue (Harrison 1971). In short the same type of mechanism that may operate to select specific components on a resource level may also determine some of the time sequence of colonization. It is worth noting, in view of the probable significance of soil animals

in spore dispersal of the later colonizers, that modifier compounds of this kind have also been regarded as important in establishing the palatibility of the leaves to components of the decomposer fauna (Heath & King 1964, Anderson 1973). One of the significant actions of the primary saprophytes may be in the metabolism of these modifier compounds resulting in increased accessibility to fungal colonization and palatability to soil animals.

The soil animals may affect the colonization process by micro-organisms in another important fashion—by their comminutive action. This is discussed more fully by Hargraves in this volume but three possible points of significance should be emphasized here. (1) The addition of specific nutrients of which nitrogenous materials such as urea or uric acid may be the most significant (Hudson 1968). (2) A process of inoculation, homogenizing and localizing the microfloral components. (3) Increasing the surface area of the resources by the reduction of particle size thereby creating a wider range of micro-environments for the microflora. This latter may have particular significance for the bacteria and actinomycetes which lack the capacity of the mycelial fungi to directly penetrate plant materials and are characterized more by surface habitats. But it may also be a feature which is of selective value to the secondary RN fungi. The nett effect of the intervention of the soil animals is to divert the primary resource succession on to a typical coprophilous path (Nicholson *et al.* 1966).

The factors determining the disappearance of species

The decline in the relative abundance of individual species, its disappearance from membership of the active microflora and the general decrease in fungal species diversity within the macrocommunity can all be related to a progressive increase in competition between the constituent species of the community. The depletion of the energy and carbon resource leads to increasing overlap in substrate-determined niches and thus to increased competition for the remaining substrates, notably cellulose and lignin. This is illustrated in Fig. 8.6. It is no doubt significant that the most persistent fungal flora includes components that have the highest capacity for the production of antibiotics (the penicillia) and the widest range of enzymatic diversity (the basidiomycetes). Webster and his co-workers have demonstrated the way in which antagonistic phenomena may increase during the decomposition of herbivore faeces (Webster 1970) and this feature is probably widespread on a variety of resources.

It is interesting to speculate briefly on the differing patterns of response that may be observed in different groups of fungi to the impact of increasing competition.

The phylloplane members of the early leaf colonizers appear to have a 'tight' cycle between inoculation and sporulation (see Fig. 8.6). By means either of resistant chlamydospores persisting on twigs and buds or by the timing of sporulation on leaf litter to coincide with bud opening they are rapidly re-established in the position on the leaf surface which ensures their early colonizing role. The life-cycle of the RS component is longer and typically seems based on a more seasonal pattern correlated with leaf litter fall as mentioned above. It is probable therefore that fruiting in these species will be environmentally controlled rather than endogenous. Interesting variants in this type of life-cycle may occur between species which occupy either rapid or slow decomposing litter, e.g. ash versus beech. In the case of rapidly decaying leaves there may be a resting resistant stage between the formation of ascocarps or pycnidia (resource determined) and the release of spores (which will be determined by the seasonal physical environment). Again this seems a promising area for investigation.

An endogenously regulated tight life-cycle, resembling that described above for the phylloplane organisms, has been described by Harper and Webster (1964) for the mucoraceous species that are pioneers on the coprophilous succession. It is possible that this group may exhibit a similar pattern of behaviour on primary resources even though they are associated with the terminal rather than the pioneer stages of decay. A repeated pattern of short time span between spore and spore will effectively 'avoid' competition. It is also likely that their increased abundance late in decomposition is correlated with the intervention of soil animals and the constant opening of 'pioneer' microhabitats. The type of behaviour exhibited by these species may fall within the category of r-selected species as defined for other groups of organisms (Pianka 1970) and also represent most clearly the behaviour of 'fugitive species' as mentioned earlier. The basidiomycetes have a contrasting behaviour more reminiscent of K-selection. They are probably the most persistent of all the fungi, colonizing soon after leaf fall and remaining of importance into the terminal and even humic stages of decay. Fruiting in the basidiomycetes requires the diversion of very considerable resources. Perennial fruit bodies or repetitive fruiting at the same site is also common in these fungi. Again the seasonal pattern of fruiting is probably associated with rapid colonization after litter fall although most isolation studies fail to confirm this. Basidiomycete mycelia are probably larger in size and more perennial in nature than those of most other fungi, which is further indicative of their competitive success. A considerable potential exists for examining the ecological role of different micro-organisms within the type of life-cycle strategies they exhibit.

The origin of unit-communities

The problem was posed earlier as to what was the basis of the hypothesized variety of unit-communities found associated with a resource. One answer may be sought in the potential for variation in the circumstances of colonization coupled with the enormous abundance of resource available to the microflora. This can be seen by considering the example of wood decay. The decomposition of branch wood is initiated in the canopy and in contrast to the deciduous leaf litter of temperate climates the input of dead branches to the decomposer system occurs continuously through the year. Potential colonization courts therefore become exposed at random points in a very extensive spatial and temporal volume. Variations in the temporal and spatial distribution of potential colonizers in the air spora could therefore lead to considerable diversity in the initiating microflora, and thus to a diversity of unit-communities by the time the decaying branches have reached the litter layer—by which time some 40% decomposition may have occurred. Whether such diversity occurs in other resources is less certain. The greater seasonality in leaf and root death and the select nature of the phylloplane and rhizoplane microfloras suggest that a more homogenous distribution may be characteristic of these resources. However, the same potential for 'opportunistic' colonization may exist once senescence and death have occurred and before substrate-limitation imposes high competition on the process of occupation.

It is probable that the features determining the variation in unit-community composition should be sought on a scale between that of the microhabitat and the macrohabitat. The demonstration, for instance, of pattern at the 10–20 cm scale in the distribution of nutrients in soils (Usher, this volume, Chapter 4) may be indicative of the types of variation that could influence the pattern of colonization of different units of the same resource.

Conclusion; the structure of microbial communities

The main elements of the structure of the microbial community of terrestrial decomposer habitats are pictured in Fig. 8.3. The fundamental unit of primary decomposition is an integrated community partitioned into niches determined by features of the chemical and physical make-up of the occupied resources. The passage of time and the progress of decay result in changes in composition and integrative structure of these unit-communities. Fig. 8.7 summarizes the possible nature of the shifts in niche structure that occur during decay. The declining availability and variety of substrates is to some measure compensated by the increase in physical diversity of the system

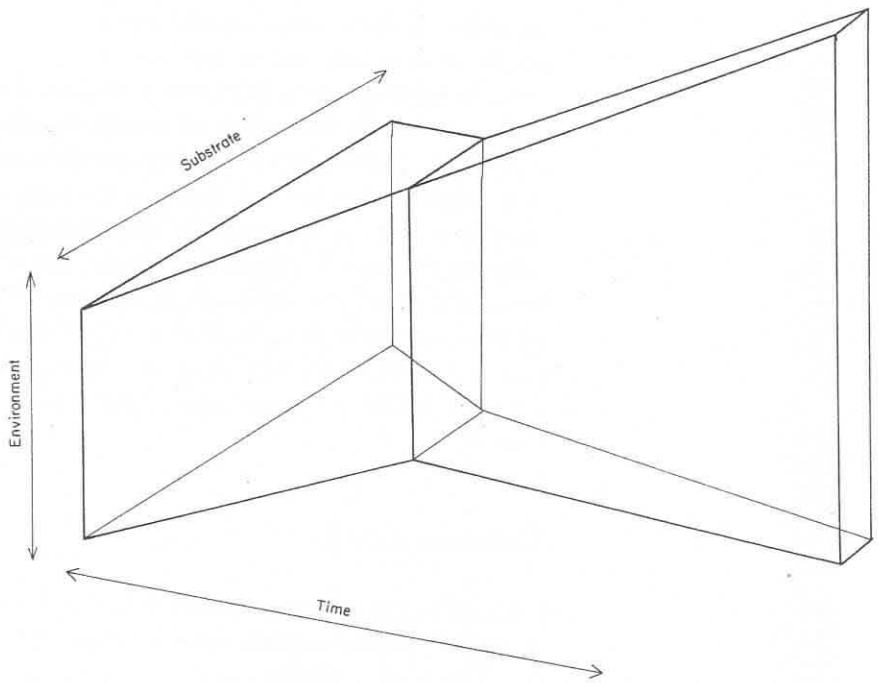

Figure 8.7. Changes in the potential variety of fundamental microbial niches within primary resources during decomposition. A cross section of the volume at right angles to any point in time represents the available niche space in relation to the two major determinants. The timescale is simplified to represent two components in decomposition; the initial rapid decomposition phase characteristic of primary resources, and the much slower decomposition of the terminal resources. These two phases are not represented in scale with regard to time.

and allows the development of a secondary microflora, that characteristic of soil rather than plant litter. In this flora bacteria and actinomycetes to a considerable extent replace the fungi which dominate litter habitats.

The proposed structure must at present be largely hypothetical. The analysis of spatial patterns of distribution of microbes in plant litter environments has been given little attention in comparison with the interest paid to time sequences or to micro-environments in the soil. However, the former would seem to be if anything the easier of experimental access.

The status of micro-organisms in decomposer food webs would seem to be determined primarily by their metabolic capacity. This is allied to a

versatility in response to rapidly changing chemical and physical environments which is reflected in their enzymic abilities, their patterns of growth and their methods of reproduction, and dispersal. This versatility is no doubt made possible by the variety of genetic mechanisms with which both the prokaryotic and eukaryotic members are endowed. However, the very versatility imposes caution on attempts to categorize micro-organisms into functional ecological groups. As with symbiotic microbes, fluctuating environments, both physical and biotic, may bring about shifts in the functional role of any one species (Lewis 1973). Thus the erection of ecological groups must be recognized as specific to the circumstance under investigation. Greater understanding of the nature of microbial community structure is likely to come from seeing it as a dynamic rather than a static concept.

Acknowledgment

I should like to acknowledge the debt that I owe to the late Ian Healey for first awakening my interest in the ecological analysis of microbial communities. I have also benefited from discussions with many colleagues of whom I should like to thank in particular Alan Hildrew, Jo Anderson and Juliet Frankland who read the paper in manuscript at various stages of preparation.

References

ALBERSHEIM P., JONES T.M. & ENGLISH P.D. (1969) Biochemistry of the cell wall in relation to infective processes. *Ann. Rev. Phytopath.* **7**, 171–94.

ANDERSON J.M. (1971) Observations on the vertical distribution of Oribatei (Acarina) in two woodland soils. In: *IV Colloquium Pedobiologiae, C.R. 4eme Coll. Int. Zool. Soc. Ed. INRA*, pp. 257–72. Paris.

ANDERSON J.M. (1973) The breakdown and decomposition of sweet chestnut (*Castanea sativa* Mill.) and beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodland soils. II. Changes in the carbon, hydrogen, nitrogen and polyphenol content. *Oecologia* **12**, 275–88.

BAILEY P.J., LIESE W. & ROSCH R. (1968) Some aspects of cellulose degradation in lignified cell walls. In: *Biodeterioration of materials.* eds. A.H. Walters & J.J. Elphick, pp. 546–57. Elsevier, Amsterdam.

BIER J.E. (1963) Tissue saprophytes and the possibility of control of some tree diseases. *Forestry. Chron.* **39**, 82–4.

BURGES A. (1960) Time and size as factors in ecology. *J. Ecol.* **48**, 273–85.

BROWN J.C. (1958) Soil fungi of some British sand dunes in relation to soil type and succession. *J. Ecol.* **46**, 641–64.

CALDWELL R. (1963) Observations on the fungal flora of decomposing beech litter in soil. *Trans. Br. mycol. Soc.* **46**, 249–61.

CHAN E.C.S., KATZNELSON H. & ROUATT J.W. (1963) The influence of soil and root extracts on the associative growth of selected soil bacteria. *Can. J. Microbiol.* **9**, 187–97.

CHRISTENSEN M. (1969) Soil microfungi of dry to mesic conifer-hardwood forests in Northern Wisconsin. *Ecology* **50**, 9–27.

DIX N.J. (1964) Colonisation and decay of bean roots. *Trans. Br. mycol. Soc.* **47**, 285–92.

EICKER A. (1973) The mycoflora of *Eucalyptus maculata* leaf litter. *Soil Biol. Biochem.* **5**, 441–8.

ENEBO L. (1963) Symbiosis in thermophilic cellulose fermentation. *Nature, Lond.* **163**, 805.

FINDLAY W.P.K. (1940) Studies in the physiology of wood-destroying fungi. III. Progress of decay under natural and controlled conditions. *Ann. Bot. NS.* **4**, 701–12.

FLANAGAN P.W. & SCARBOROUGH A.M. (1974) Physiological groups of decomposer fungi on Tundra plant remains. In: *Soil Organisms and decomposition in tundra*, eds. A.J. Holding, O.W. Heal, S.F. Maclean Jnr., P.W. Flanagan, pp. 159–81. Tundra Biome Steering Committee. Stockholm.

FRANKLAND J.C. (1966) Succession of fungi on decaying petioles of *Pteridium aquilinum*. *J. Ecol.* **54**, 41–63.

GARRETT S.D. (1951) Ecological groups of soil fungi: a survey of substrate relationships. *New Phytol.* **50**, 149–66.

GARRETT S.D. (1956) *Biology of the root-infecting fungi*. Cambridge University Press.

GARRETT S.D. (1963) *Soil fungi and soil fertility*. Pergamon, Oxford.

GRAY T.R.G. (1969) The identification of soil bacteria. In: *The Soil Ecosystem*, ed. J.G. Sheals, pp. 73–82. The Systematics Association, London.

GREGORY P.H. (1973) *The microbiology of the atmosphere*. 2nd edn. Leonard Hill, London.

GRIFFIN D.M. (1972) *Ecology of Soil Fungi*. Chapman and Hall, London.

GROSJEAN J. (1950) Substances with fungicidal activity in the bark of deciduous trees. *Nature, Lond.* **165**, 853–4.

HARPER J.E. & WEBSTER J. (1964) An experimental analysis of the coprophilous fungus succession. *Trans. Br. mycol. Soc.* **47**, 511–30.

HARRISON A.F. (1971) The inhibitory effect of oak leaf litter tannins on the growth of fungi; in relation to litter decomposition. *Soil. Biol. Biochem.* **3**, 167–72.

HAYES A.J. (1965) Some microfungi from Scots Pine litter. *Trans. Br. mycol. Soc.* **48**, 179–85.

HEAL O.W. & MACLEAN S.F. Jnr. (1975) *Comparative productivity in ecosystems—secondary productivity*. In: *Unifying concepts in ecology*, eds. W.H. Van Dobben & R.H. Lowe-McConnell, Junk, Hague and Purdo, Wageningen (in press).

HEALEY I.N. & SWIFT M.J. (1971) Aspects of the accumulation and decomposition of wood in the litter of a coppiced Beech–Oak woodland. In: *IV Colloquium Pedobiologiae, C.R. 4eme Coll. Int. Zool. Soc.* Ed. INRA, pp. 417–30. Paris.

HEATH G.W. & KING H.G.C. (1964) Litter breakdown in deciduous forest soils. *8th Int. Congr. Soil Sci.* **3**, 979–87.

HEDGER J.N. & HUDSON H.J. (1974) Nutritional studies of *Thermomyces lanuginosus* from wheat straw compost. *Trans. Br. mycol. Soc.* **62**, 129–43.

HENDERSON M.E.K. (1960) Studies on the physiology of lignin decomposition by soil fungi. In: *The ecology of soil fungi*. eds. D. Parkinson & J.S. Waid, pp. 286–96. Liverpool University Press.

HERING T.F. (1965) Succession of fungi in the litter of a Lake District oakwood. *Trans. Br. mycol. Soc.* **48**, 391–408.

HERING T.F. (1967) Fungal decomposition of oak leaf litter. *Trans. Br. mycol. Soc.* **50**, 267–73.

HINTIKKA V. (1970) Selective effects of terpenes on wood-decomposing Hymenomycetes. *Karstenia* 11, 28–32.

HISSETT R. & GRAY T.R.G. (1974) Bacterial populations of litter and soil in a deciduous woodland. I. Qualitative studies. *Rev. Ecol. Biol. Sol.* 4, 495–508.

HOGG B.M. & HUDSON H.J. (1966) Micro-fungi on leaves of *Fagus sylvatica*. 1. The micro-fungal succession. *Trans. Br. mycol. Soc.* 49, 185–92.

HUDSON H.J. (1968) The ecology of fungi on plant remains above the soil. *New Phytol.* 67, 837–74.

HUDSON H.J. (1970) Infraspecific categories in fungi. *Biol. J. Linn. Soc.* 2, 211–19.

HULME M.A. & STRANKS D.W. (1971) Regulation of cellulase production by *Myrothecium verrucaria* grown on non-cellulosic substrates. *J. gen. Microbiol.* 69, 145–55.

KENDRICK W.B. & BURGES A. (1962) Biological aspects of the decay of *Pinus sylvestris* leaf litter. *Nova. Hedwig.* 4, 313–42.

KING N.J. (1966) The extracellular enzymes of *Coniophora cerebella*. *Biochem. J.* 100, 784–92.

KING N.J. & FULLER D.B. (1968) The xylanase system of *Coniophora cerebella*. *Biochem. J.* 108, 571–6.

KIRK T.K. (1971) The effects of micro-organisms on lignin. *Ann. Rev. Phytopath.* 9, 185–210.

LEWIS D.H. (1973) Concepts in fungal nutrition and the origin of biotrophy. *Biol. Rev.* 48, 261–78.

MACARTHUR R.H. (1972) *Geographical ecology; patterns in the distribution of species*. Harper & Row, London.

MACARTHUR R.H. & WILSON E.O. (1967) *The theory of Island Biogeography*. Princeton University Press, New Jersey.

MARTIN J.T. & JUNIPER B.E. (1970) *The cuticles of plants*. Edward Arnold, London.

MERRILL W. & COWLING E.B. (1966) Role of nitrogen in wood deterioration: amounts and distribution of nitrogen in tree stems. *Can. J. Bot.* 4, 1555–80.

MINDERMAN G. (1968) Addition, decomposition and accumulation of organic matter in forests. *J. Ecol.* 56, 355–62.

NICHOLSON P.B., BOCOCK K.L. & HEAL O.W. (1966) Studies on the decomposition of the faecal pellets of a millipede (*Glomeris marginata* Villers). *J. Ecol.* 54, 755–66.

NORTHCOTE D.H. (1972) Chemistry of the plant cell wall. *Ann. Rev. Plant. Physiol.* 23, 113–32.

NOVACK R.D. & WHITTINGHAM W.F. (1968) Soil and litter microfungi of a maple-elm-ash floodplain community. *Mycologia.* 60, 776–87.

PARK D. (1960) Antagonism—the background to soil fungi. In: *The ecology of soil fungi*, eds. D. Parkinson & J.S. Waid, pp. 148–59. Liverpool University Press.

PARK D. (1968) The ecology of terrestrial fungi. In: *The Fungi*, Vol. III, eds. G.C. Ainsworth & A.S. Sussman, pp. 5–39. Academic Press, London.

PARKINSON D., TAYLOR G.S. & PEARSON R. (1963) Studies on fungi in the root region. I. The development of fungi on young roots. *Plant and Soil* 19, 332–49.

PIANKA E.R. (1970) On r- and K-selection. *Am. Naturalist.* 104, 592–7.

PRIESTLEY C.A. (1962) Carbohydrate resources within the perennial plant. Commonwealth Bureau of Horticulture and Plantation Crops. *Tech. Comm.* 27, 116 pp.

PUGH G.J.F. (1962) Studies on fungi in coastal soils. II. Fungal ecology in a developing salt marsh. *Trans. Br. mycol. Soc.* 45, 560–6.

PUGH G.J.F. & BUCKLEY N.G. (1971) *Aureobasideum pullulans:* an endophyte in sycamore and other trees. *Trans. Br. mycol. Soc.* 57, 227–31.

PUGH G.J.F., BUCKLEY N.G. & MULDER J. (1972) The role of phylloplane fungi in the early colonisation of leaves. *Symp. Biol. Hung.* **11**, 329–33.

REESE E.T. (1968) Microbial transformation of soil polysaccharides. In: *Organic Matter and Soil Fertility*, pp. 535–77. North Holland, Amsterdam.

RISHBETH J. (1951) Observations on the biology of *Fomes annosus* with particular reference to East Anglian pine plantations. II. Spore production, stump infection and saprophytic activity in stumps. *Ann. Bot., Lond. N.S.* **15**, 221–76.

SCHEFFER T.C. & COWLING E.B. (1966) Natural resistance of wood to microbial deterioration. *Ann. Rev. Phytopathology* **4**, 147–70.

SELBY K. (1968) Mechanism of biodegradation of cellulose. In: *Biodeterioration of materials*, eds. A.H. Walters & J.J. Elphick, pp. 62–78. Elsevier, Amsterdam.

SIMPSON E.H. (1949) Measurement of diversity. *Nature Lond.* **163**, 688.

SUNDMAN V. (1970) Four bacterial soil populations characterised and compared by a factor analytical method. *Can. J. Microbiol.* **16**, 455–64.

SWIFT M.J. (1976) The ecology of wood decomposition. *Sci. Progress* (Oxford) (in press).

SZABO I.M. (1974) *Microbial communities in a forest-rendzina ecosystem; the pattern of microbial communities*. Akademiai Kiado, Budapest.

TENNEY F.G. & WAKSMAN S.A. (1929) Composition of natural organic materials and their decomposition in the soil. IV. The nature and rapidity of decomposition of the various organic complexes in different plant materials, under aerobic conditions. *Soil Sci.* **28**, 55–84.

THORNBER J.B. & NORTHCOTE D.H. (1961a) Changes in the chemical composition of a cambial cell during its differentiation into xylem and phloem tissue in trees. 1. Main components, *Biochem. J.* **81**, 449–54.

THORNBER J.B. & NORTHCOTE D.H. (1961b) Changes in the chemical composition of a cambial cell during its differentiation into xylem and phloem tissue in trees. 2. Carbohydrate constituents of each main component. *Biochem. J.* **81**, 455–64.

THORNBER J.B. & NORTHCOTE D.H. (1962) Changes in the chemical composition of a cambial cell during its differentiation into xylem and phloem tissue in trees. 3. Xylan, glucomannan and α-cellulose fractions. *Biochem. J.* **82**, 340–6.

TRIBE H. (1966) Interactions of soil fungi on cellulose film. *Trans. Br. mycol. Soc.* **49**, 457–66.

WAID J.S. (1974) Decomposition of roots. In: *Biology of plant litter decomposition*, eds. C.H. Dickinson & G.J.F. Pugh, pp. 175–211. Academic Press, London.

WARCUP J.H. (1965) Growth and reproduction of soil micro-organisms in relation to substrate. In: *Ecology of soil-borne plant pathogens*, eds. K.F. Baker & W.C. Snyder, pp. 52–68. John Murray, London.

WEBSTER J. (1956) Succession of fungi on decaying cocksfoot culms. (Part 1.) *J. Ecol.* **44**, 517–44.

WEBSTER J. (1970) Coprophilous fungi. *Trans. Br. mycol. Soc.* **54**, 161–80.

WEBSTER J. & DIX N.J. (1960) Succession of fungi on decaying cocksfoot culms. III. A comparison of the sporulation and growth of some primary saprophytes on stem, leaf blade and leaf sheath. *Trans. Br. mycol. Soc.* **43**, 85–99.

WHITTAKER R.H. & WOODWELL G.M. (1968) Dimension and production relations of trees and shrubs in the Brookhaven Forest, New York. *J. Ecol.* **56**, 1–25.

WICKLOW D.T. & WHITTINGHAM W.F. (1974) Soil microfungal changes among the profiles of disturbed conifer-hardwood forests. *Ecology* **55**, 3–16.

WIDDEN P. & PARKINSON D. (1973) Fungi from Canadian coniferous forest soils. *Can. J. Bot.* **51**, 2275–90.

WIDDEN P. & PARKINSON D. (1974) The effects of a forest fire on soil microfungi. *Soil Biol. Biochem.* 7, 125–38.

WIEGERT R.G., COLEMAN D.C. & ODUM E.P. (1970) Energetics of the litter-soil subsystem. Methods of study in soil ecology. *Proc. Paris Symp.*, pp. 93–8. UNESCO, Paris.

WILLIAMS S.T., DAVIES F.L. & HALL D.M. (1969) A practical approach to the taxonomy of Actinomycetes isolated from soil. In: *The soil ecosystem*, ed. J.G. Sheals, pp. 107–17. The Systematics Association, London.

WILLIAMS S.T. & GRAY T.R.G. (1974) Decomposition of litter on the soil surface. In: *Biology of plant litter decomposition*, eds. C.H. Dickinson & G.J.F. Pugh, pp. 611–32. Academic Press, London.